# NOTES ON THE LOCOMOTION OF THE NUDIBRANCHIATE MOLLUSK DENDRONOTUS GIGANTEUS O'DONOGHUE.*

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Many works have already appeared on molluscan locomotion. Thus Simroth ('79) called attention to the relation between the pedal nerve, the musculature of the foot, and the "locomotorischen Wellen" in *Limax*. Fleischmann ('85) observes: "Kontraktionswellen über die ganze Oberfläche des Fusses in *Anodonta*, hinten beginnend und nach vorn strichend." Jordan ('01), and again in 1905, records a similar feature for *Aplysia limacina*. Bohn ('02) finds that progressive movements of *Helix pomatia* L. are accomplished by undulations in the form of waves of the pedal musculature which rests against a solid or support, and that these rhythmic pedal waves are partly independent of mechanical excitations. Künkel ('03) finds that the "Wellenspiel" increases when he touches a crawling *Limax tenellus* (or *L. agrestris, L. arborum*). Carlson ('05) substantiates the findings of Jordan ('01) by describing for *Helix dupetithonarsi* a succession of large waves which pass from the head to the tail, an extraordinary mode of progression employed when the animal is in a hurry. Biedermann ('05) refers to "Querbänder" that follow one another in parallel lines on the under side of the foot of *Helix pomatia*, when this species crawls on a glass plate. Von Uexküll ('09) confirms the findings of Jordan for *Aplysia*, viz., that waves are advancing, when the foot is lifted from the ground, from the anterior to the posterior, the waves advancing in the opposite direction in *Limax* and *Helix*.

A more complete analysis of pedal locomotion among mollusks and other invertebrates has been accomplished by the brilliant works of Parker ('11, '14, '17, '17*a*, '21) and his pupil, Olmsted ('17). Parker ('11) recognizes two main sets of locomotion means for ordinary gastropods: (1) arhythmic (*Ilyanssa obsoleta*

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Say) locomotion is accomplished without pedal waves; (2) with pedal waves, or rhythmic locomotion (*Dolabrifera virens* Verrill, *Tectarius nodulosus* Gmel., *Nerita tessellata* Gmel., *Chiton tuberculatus* Linnæus, etc.). "In rhythmic locomotion the waves may run from the posterior to the anterior, that is, *direct;* or the reverse, that is, *retrograde.* The foot may exhibit one, *monotaxic;* two, *ditaxic;* or four, *tetrataxic,* series of waves. In the ditaxic foot the waves may be alternate or opposite. . . . Locomotion is the cumulative result of local forward motion on the part of one section of the foot after another till the whole foot has been moved." The essential act of pedal locomotion of all creeping gastropods may be exhibited by the retrograde wave movement on the foot of *Chiton tuberculatus,* in which, according to Parker ('14), the locomotor waves run from anterior to posterior. In this type, "The waves extend the whole width of the foot and are from five to six mm. in antero-posterior extent. They represent an area of the foot temporarily lifted from the substrate. . . . Excepting in the region of the wave, the foot is firmly attached to the substrate; hence at any moment from nine tenths to four fifths of the foot is fixed and the remainder free." Pedal locomotion of Actinians (*Metridium marginatum* Milne-Edw., *Sagartia luciæ* Verrill, *Condylactis passiflora* Duch. and Mich., and *Actinia bermudensis* Verrill) is interestingly accomplished by a wave-like movement which progresses over the pedal disc in the direction of locomotion (Parker, '17). "In the actinian locomotor wave each point on the pedal disc is successively raised from the substratum, moved forward, and put down." Writing on the locomotion of the sea-hare, *Aplysia californica* Cooper, this same author ('17*a*) says: "Pedal locomotion in *Aplysia* is due to monotaxic retrograde waves which lift the foot locally and temporarily from the substrate, making it thus to move forward with freedom, while the rest of the foot for the time being holds the snail in place by many small areas of local suction. The portion of the foot that moves forward is the elevated region," pp. 143 and 144. Locomotion in the holothurian *Stichopus panimensis* Clark is effected by direct monotaxic waves (Parker, '21). That is, "Creeping is accomplished in part by a muscular wave that originates at the posterior end of the animal and sweeps over it to the anterior." It is inter-

esting to note that locomotion in this echinoderm is in essentials of that type of gastropod locomotion which has been designated the direct monotaxic type.

Olmsted ('17) finds in the huge slug *Veronicella schivelyoe* Pilsb. there are always about eleven pedal waves which pass from the posterior to the anterior and extend the full width of the foot; this is direct monotaxic locomotion. In *Onchidium floridanum* only one or two waves are shown at a given time. In *Eulota simularis* Fer. the average number of waves are 9 à 10. *Helcinia convexa* Pfr., *Tethys dactylonula* Rang, and *Fissurella nodosa* Born show retrograde monotaxic locomotion. *Tectarius misricatus* L. exhibits retrograde alternate ditaxic locomotion. *Tritonidea tincta* and *Columbella mercatoria* L. are retrograde tetrataxic in their locomotion. *Cypræa exanthema* L. shows long and short lateral waves which move either to the right or left; complete diagonal waves which move to the right or left, and retrograde waves from the anterior edge to the center of the foot and extends to the posterior. Finally, *Marginella arena* Val., *Haminea antillarum* Orb., and *Bulla occidentalis* A. Ads. move by ciliary action alone. Retrograde pedal waves, according to Crozier ('19), are the means of locomotion in *Ischnochiton purpurascens* Ad., *Acanthochites spiculosus* Reeve, and *Tonicia* sp.; the first-named one also exhibits a "gallop" like that of *Helix,* which is independent of the pedal waves.

The remarkable nudibranch *Dendronotus giganteus* has recently been described (1921) from the Vancouver Island region by Dr. Chas. H. O'Donoghue. This author records four species of this genus: *D. arborescence* Müller, *D. dalli* Bergh, *D. giganteus* O'Donoghue, and *D. rufus* O'Donoghue, from this region. The largest of these species measured: 50 mm. long by 15 mm. high by 15 mm. broad; 31 mm. by 9 mm. by 6 mm.; 140 mm. by 43 mm. by 33 mm.; and 14 mm. by 4.5 mm. by 4 mm., respectively. According to this author, a preserved specimen of *D. giganteus* in the laboratory obtained by Professor C. M. Fraser, 1913, measured 210 mm. long by 84 mm. high by 55 mm. wide. Allowing for approximately the same amount of shrinkage, according to O'Donoghue, the specimen when alive must have reached the size of 260 mm. long by 100 mm. high and 65 mm. broad. This is indeed a

gigantic size for a nudibranch! It is matter of common knowledge, however, that the fauna of the North American Pacific coast attain not only a large size, but are in fact very abundant and diversified. (*Vide:* Kjerschow Agersborg, 1920.)

Large specimens of this genus also occur in the vicinity of Puget Sound Biological Station, Friday Harbor, Washington. Thus during the summer of 1913 a collecting party from the station found on the shore of Shaw Island (not very far from Canoe Island) a large specimen which must have measured about 200 mm. in length. To the writer's knowledge no one identified the specimen at that time. It was conveniently classed *D. arborescence.*

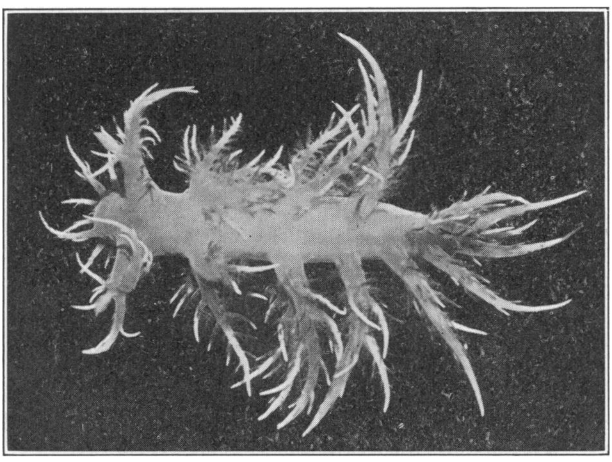

FIG. 1. Photograph of *Dendronotus giganteus* O'Donoghue, dorsal view.

During the summer of 1921 I again visited the Puget Sound Biological Station. On July 20 I found a very fine specimen of *Dendronotus* between the logs of the floating dock of the station (Figs. 1–4). Upon examination it was found to fit perfectly to the description of O'Donoghue for *D. giganteus.* It measured 140 mm. long by 60 mm. high by 40 mm. broad. The foot was 90 mm. long and 40 mm. wide at its widest part. This specimen was kept alive in the laboratory for three weeks. During this time it did not feed, as far as I know, on anything. I tried to feed it on crustaceans, echinoderm gonads, cœlenterate tentacles, green algæ,

etc., but it refused all these except once, in which case it opened its large fleshy lips in response to the touch of cœlenterate tentacles, took them within its mouth, only to be ejected a little later. When the animal was first found, and for several days afterwards, its stomach was filled with air, which aided it in floating. It was

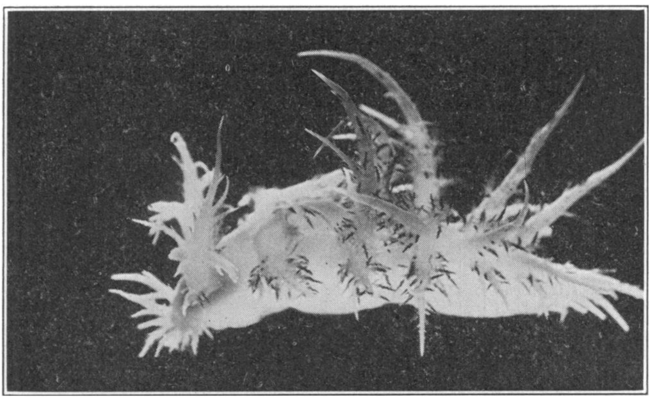

FIG. 2. Photograph of *Dendronotus giganteus* O'Donoghue, lateral view.

able, however, to submerge itself while in this condition. When the air bubbles contained in the stomach after a few days had disappeared, a little by little, the animal was able to float nevertheless.

In conjunction with the study of qualitative chemical and physical stimulations in *Hermissenda opalescence* Cooper, I also studied *D. giganteus* (*vide* Kjerschow Agersborg, 1922*a*; for a full description of the species: O'Donoghue, 1921), and noticed incidentally its remarkable mode of locomotion. During the first few days in the laboratory it was very active, and it was quite difficult to make proper observations on its response to stimuli; on the other hand, it offered the opportunity to study its mode of locomotion which is appended.

*Dendronotus giganteus* has two distinct modes of locomotion. The one, and the most commonly used, is that of swimming; the other is creeping. The swimming movements are effected by a regular twisting of the body in an undulatory manner, beginning at the anterior end and passing gradually to the posterior. These

movements are alternated from side to side. The lashing of the anterior part of the body from side to side is relatively powerful and a much more rapid progressive movement is effected over that attained by creeping. The undulatory movements employed in swimming start with the head being bent downward and sideways, forming a wave-like twist in the side of the body-wall like that in a blade of a propeller. This wave passes gradually toward the posterior end (Figs. 3–4), and disappears when the animal makes

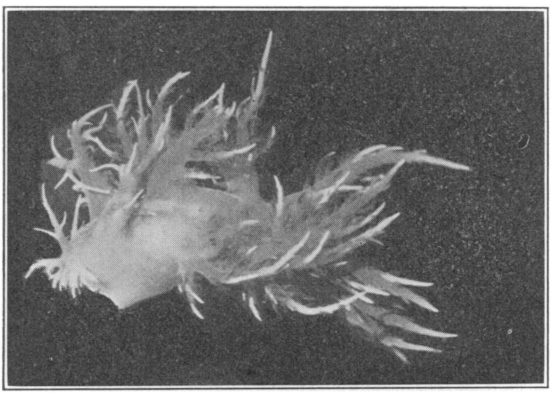

FIG. 3. Photograph of *Dendronotus giganteus* O'Donoghue in the act of swimming; the head has returned from its bend to the right, and the twist-like wave is shown in the side passing toward the posterior end.

the next stroke to the opposite side. When the animal makes a stroke to the right the posterior two thirds is bent so as to form an angle of 45° with the anterior one third. But the posterior part of the body also rotates about 45° from the vertical plane, so that the left side with the foot forms a large wave which sweeps posteriorly, while the anterior part of the body, in front of the wave, is kept vertically. When the animal makes a stroke to the left, the same phenomenon is repeated on the right side. An animal may cover a distance of 30 cm. in a few seconds, making side-strokes of about 45 a minute.

The creeping method of locomotion was seldom employed. If the animal was forced to the bottom of the dish, it would attach itself to the substratum and commence gliding along imperceptibly. Close observation brought to light, however, a succession of undu-

lations which passed from the posterior end of the foot to the anterior. The animal adhered to the substratum by sucking to the extent that it did not pass out of the dish when the water was poured out of it. In creeping, local undulations are set up in the

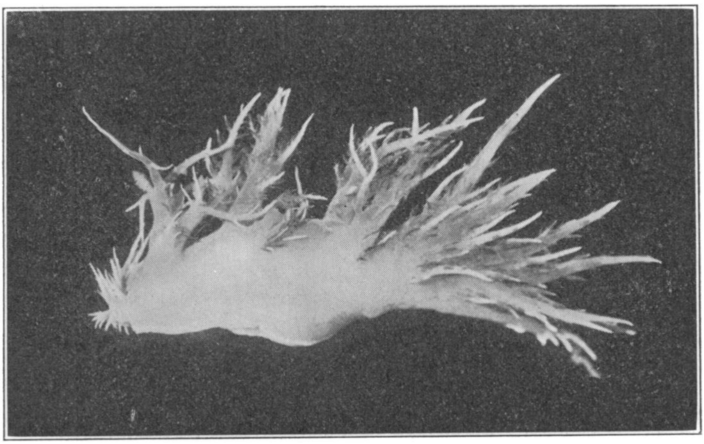

FIG. 4. Photograph of *Dendronotus giganteus* O'Donoghue showing the locomotor wave during swimming passing toward the posterior end. All the photographs are of living specimens, photographed through the water, by Dr. Myrtle E. Johnson, State Teachers College, San Diego, Calif. The photographs were taken at the Puget Sound Biological Station, July, 1921.

form of series of areas adhering to the substratum, and intervened by non-adhering parts which travel gradually toward the anterior end. The method of creeping may be classed as direct rhythmic locomotion, to use the terminology of previous writers on this subject, although it is not possible to classify this exactly at this time. The method of rhythmic locomotion is accompanied in this case, I believe, by ciliary action. The foot in *Dendronotus giganteus* is highly ciliated. No slime is produced during locomotion or at any other time. The foot is also uniformly ciliated in *Melibe leonina* Gould (Kjerschow Agersborg, 1921*a*, 1922). Ordinary locomotion in *Melibe* is effected by the ciliary action of the foot. The ciliated epithelium is innervated with nerve fibers from the pedal nerve-net (Kjerschow Agersborg, 1922).

Swimming as a means of locomotion is common among pelagic forms which are then frequently provided with secondary organs

for that purpose as in *Aplysis* Linnæus, in which the parapodia figure quite prominently. Forms closely related to the nudibranchs, such as the gymnosomatous *Pteropoda,* may be particularly exemplified in this connection. These parapodic forms are pelagic *per se* (*vide* Kjerschow Agersborg, 1922*c*). Although several nudibranchs are pelagic, this habit is secondary, notwithstanding.

Collingwood ('79) records swimming as a means of locomotion in *Scyllea pelagica,* and Garstang ('90) for *Lomanotus* Verany. Kjerschow Agersborg ('19, '21, '22, '22*b*) reports swimming as one mode of locomotion in *Melibe leonina.* But none of the forms as here mentioned are good swimmers although Garstang's statement seems to indicate that *Lomanotus* progresses through the water during swimming. I am unaware of any previous record as to the pelagic habit of *Dendronotus.* The assumption may be quite justified that *Dendronotus,* in spite of its highly developed foot, is pelagic in habit, not only because of the evidence connected with the place of discovery of the particular specimen upon which this discussion is based, but rather on the striking, highly developed method of locomotion, viz., swimming. *Melibe leonina,* although quite frequently pelagic in habit, is not such an able swimmer as *Dendronotus giganteus.* The last-named species may, therefore, be more pelagic in habit than it is commonly thought to be.

Simroth, Fleischmann, Jordan, Bohn, Künkel, Carlson, Biedermann, von Uexküll, and others have shown that during ordinary locomotion not only do the muscle fibers of the foot take part in the production of the pedal waves, but also certain muscle fibers of the body-wall. This is more readily understood when one realizes the relation of the muscle fibers of the body-wall to those in the foot, in terrestrial as well as in aquatic or marine snails. The swimming habit, of course, is not equally developed in all, which is partly due to the general shape of the body. During swimming the muscle fibers of the body-wall act preëminently; during creeping, those of the foot.

## Summary.

1. *Dendronotus giganteus* O'Donoghue swims by bending the anterior end of the body sideways to an angle of about 45°, pro-

ducing each time a powerful stroke by the head, and forming in the right or left side of the body-wall, according to the bend of the head, a large twisted muscular wave which passes toward the posterior. By the sweep of these waves locomotion is effected. Of all known non-parapodic nudibranchs, *Dendronotus giganteus* is the most able swimmer.

2. Creeping is effected by direct rhythmic waves augmented by ciliary action of the foot.

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